

EFFECTS OF COBBLE EMBEDDEDNESS ON THE MICRODISTRIBUTION OF THE SCULPIN *COTTUS BELDINGI* AND ITS STONEFLY PREY

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ABSTRACT.—Laboratory experiments were undertaken to assess the effects of three levels of cobble embeddedness on the microdistribution of the sculpin *Cottus beldingi* and its stonefly prey, *Skwala americana*. Experiments were conducted separately and together as predator and prey in temperature- and flow-controlled artificial streams. When tested either separately or together, both the predator sculpin and its stonefly prey occurred in significantly greater numbers on substrata having unembedded cobbles than substrata having half- or completely embedded cobbles. Stonefly densities were greater in substrata having unembedded cobbles even though predator densities within the more embedded cobble patches were significantly lower. These findings support the hypothesis that higher predator densities influence prey densities less than the structural habitat quality of unembedded-cobble patches.

Key words: predator-prey, cobble embeddedness, nonlethal effects, stoneflies, sculpins, nonpoint source sedimentation, *Cottus beldingi*.

Reduced summer flows and increased sedimentation in many western North American streams may significantly diminish the size and availability of adequate microhabitat patches for benthic fish and insects. Sedimentation from agricultural sources has been linked to pronounced changes in the trophic structure of lotic fish assemblages (Berkman and Rabeni 1987) and may affect macroinvertebrate community structure, further altering trophic relations within the lotic food web.

Such trophic changes, in part, may result from alterations in prey refugia brought about by the embeddedness of cobble substrata. Brusven and Rose (1981) found that cobble embeddedness significantly influenced the vulnerability of two insect predators, *Hesperoperla pacifica* (Plecoptera: Perlidae) and *Rhyacophila vaccua* (Trichoptera: Rhyacophilidae), to predation by *Cottus rhotheus*. They suggested high sculpin predation success in the embedded substrata was due to the loss of macroinvertebrate refugia under cobbles.

Microhabitat shifts by macroinvertebrate prey in response to vertebrate and macroinvertebrate predators have been reported by several workers (Stein and Magnuson 1976, Stein 1977, Peckarsky and Dodson 1980, Peckarsky 1983). Feltnate et al. (1986) found

that, under laboratory conditions, *Paragnetina media* (Plecoptera: Perlidae) selected larger substrata over smaller ones in the presence of rainbow trout.

Sculpins hold a significant position in the food web of Pacific Northwest stream communities and have been shown to reduce food resources, food consumption, and the production of trout (Brocksen et al. 1968). *Cottus beldingi*, the Paiute sculpin, is the most abundant fish species in Lapwai Creek (Kucera et al. 1983), the stream investigated in this study. This ambush predator feeds almost exclusively on benthic macroinvertebrates (Johnson 1985). Finger (1982) reported that adult *C. beldingi* preferred coarse-grained substrata in an Oregon stream. In California, Gard and Flittner (1974) found the highest densities of *C. beldingi* in rubble or gravel substrata.

Skwala americana (Plecoptera: Perlodidae) is a common lotic stonefly found throughout western North America (Baumann et al. 1977). Nymphs are important prey of *C. beldingi* (Johnson 1985) and are normally found in relatively unconsolidated, unembedded-cobble riffles (Short and Ward 1980). They commonly feed on small mayflies and midges (Fuller and Stewart 1977, Richardson and Gaufin 1971). *Skwala americana* is univoltine, with adult

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emergence occurring from February through July (Baumann et al. 1977).

The purpose of this study was to determine the microdistribution of *C. beldingi* and *Skwala americana*, both separately and together as predator and prey, when given choices among three levels of cobble embeddedness in an artificial stream.

MATERIALS AND METHODS

Field Collection

Lapwai Creek (46° 18'N, 116° 43'W) drains agricultural land in the Columbia River Basin 20 km east of Lewiston, Idaho. Field estimates of sculpin density were made in September 1987 from riffles in Lapwai Creek and its tributaries. Sculpins were frightened into a drift net attached to two wire-mesh side-wings that sampled a rectangular 0.44-m² area. Adult sculpins (66.1 ± 9.4 mm) used in the experiment were collected during September and October 1987.

Late-instar stonefly nymphs (*Skwala americana*) were collected with kick nets from the same riffles from which sculpins were collected. The nymphs were transported to the laboratory.

Preconditioning of Test Organisms

Sculpins and stoneflies were acclimated in laboratory streams like those described by Brusven (1973). Cobbles were placed in the streams to provide cover. All organisms were acclimated for at least 48 h in holding streams before each experiment. Sculpins were randomly selected 24 h before each experiment, isolated, and starved to better elicit hunger and foraging behavior.

Experimental Stream Channels

Two Plexiglas® streams (3.35 × 0.25 × 0.20 m) were arranged side by side in the lab-

oratory. The streams were partitioned into three 0.19-m² sections bordered by a 0.04-m² sand area at each end (Fig. 1).

Unchlorinated tapwater was recirculated through the channels by electrical pumps (mean velocity, 2.44 cm s⁻¹). Water temperature was maintained at 13.9°C with thermostatic refrigeration units placed within recirculating sumps. Water depth was held at 13.0 cm above the base substrate, thus assuring that all cobbles were fully submersed.

Substrate Treatments

Natural stream cobbles (62.0–127.0 mm, principal axis) were collected from Lapwai Creek. Cobbles were scrubbed with a brush under hot tap water, dried, and labeled with an identification number and orientation arrow to enable replication of their spatial arrangement in either an unembedded or half-embedded condition. Fifteen cobbles were randomly positioned in each of the test sections of the stream except for the simulated, fully embedded condition, which had no visible surface presence of cobbles. The cobbles covered ca. 60% of the two-dimensional area of the unembedded and 50%-embedded sections.

To simulate a 50%-embedded condition, half of each cobble's principal axis was cast in plaster of paris. The casts were later filled with a mixture of concrete and natural stream sand. After drying, the "half-casts" were textured with a wire brush and assigned an identification number and directional arrow that corresponded to their natural-rock counterparts.

Two centimeters of washed stream sand was spread over the bottom of each artificial stream to serve as a base substratum. Three cobble-embeddedness conditions were randomly assigned among three stream sections. In one section cobbles were placed on top of the sand. In another section the "half-casts"



Fig. 1. Schematic diagram of an artificial channel showing the stream sections and one cobble-embeddedness arrangement: (U) = unembedded cobbles, (H) = 50%-embedded cobbles, (S) = 100%-embedded cobbles, and (B) = sand buffer zones.

were positioned in the identical arrangement and orientation as their natural unembedded counterparts. They were placed directly on the sand, thereby limiting access to their under surfaces by the organisms studied. The remaining section was left as a 2.0-cm layer of sand and simulated a 100% cobble-embedded condition with no cobbles evident on the surface.

Experimental Trials

Experimental trials ran for 20 h and were terminated at sunrise (photoperiod, 9 light: 11 dark). Upon completion of a trial, water flow was shut off and partitions were placed between stream sections. Test organisms were recovered from each section and counted. Animals recovered from the buffer sections were not included in the statistical analysis. Two experiments were conducted: (1) predator and prey were tested independently to assess noninteractive distribution, and (2) predator and prey were tested together to assess interactive distribution.

PREDATOR AND PREY—NONINTERACTIVE.—This experiment examined habitat selection by the predator (sculpin) and prey (stonefly) in absence of each other. Two parallel streams were used, one for the predator and one for the prey. Equal numbers of sculpins (2) and stoneflies (4) were introduced into each section (3 sections/stream) of the respective streams and allowed to freely distribute among the sections for 20 h. Sculpin stocking density in the artificial channel (6 fish/channel) approximated sculpin density in the field, i.e., 6.9 fish m^{-2} (Haro 1988).

Three cobble-embedded conditions were randomly assigned among stream sections

(i.e., upstream, midstream, and downstream). Each possible cobble arrangement was replicated randomly in time (three times) for a total of nine trials for each organism. A non-parametric Kruskal-Wallis test with a posteriori pairwise comparisons (Conover 1980) was used to detect significant differences among mean-ranked numbers of organisms recovered from three cobble-embeddedness conditions (Conover 1980).

PREDATOR AND PREY—INTERACTIVE.—This experiment examined predator-prey interaction when both the predator and prey were introduced into a common stream. Four stoneflies were placed into each of three sections 1 h prior to the introduction of sculpins (2/section, 6/stream). In this experiment, trials were run concurrently in two parallel streams. Each possible cobble arrangement (three) was replicated in time (four times) for a total of 24 trials. This experiment assessed whether distribution of either the sculpin predator or its prey was altered in the presence of the other species. Statistical tests similar to those described in the first experiment were used to detect significant differences among mean-ranked numbers of organisms from three cobble-embeddedness conditions.

RESULTS

Predator and Prey—Noninteractive

Sculpin numbers (Table 1) were significantly different between substrate-embeddedness conditions ($P < .001$) when tested in absence of stonefly prey. Multiple comparisons showed that mean-ranked sculpin

TABLE 1. Kruskal-Wallis test statistic (T) and mean-ranked sculpin and stonefly counts (R_i/n_i) among cobble-embeddedness conditions. Unique lowercase letters denote significantly different counts within both noninteractive and interactive predator and prey experiments.

Treatment	Sculpin		Stonefly	
	T	R_i/n_i	T	R_i/n_i
Noninteractive ($n_i = 18$)	53.03***		53.16***	
Unembedded		4.88a		8.06a
50%-embedded		1.50b		3.17b
100%-embedded		1.33b		1.39c
Interactive ($n_i = 24$)	71.05***		71.10***	
Unembedded		5.83a		5.63a
50%-embedded		1.58b		2.75b
100%-embedded		1.38b		1.33c

***Kruskal-Wallis test error rate: $P \leq .0001$. Multiple comparison error rate: $P \leq .005$.

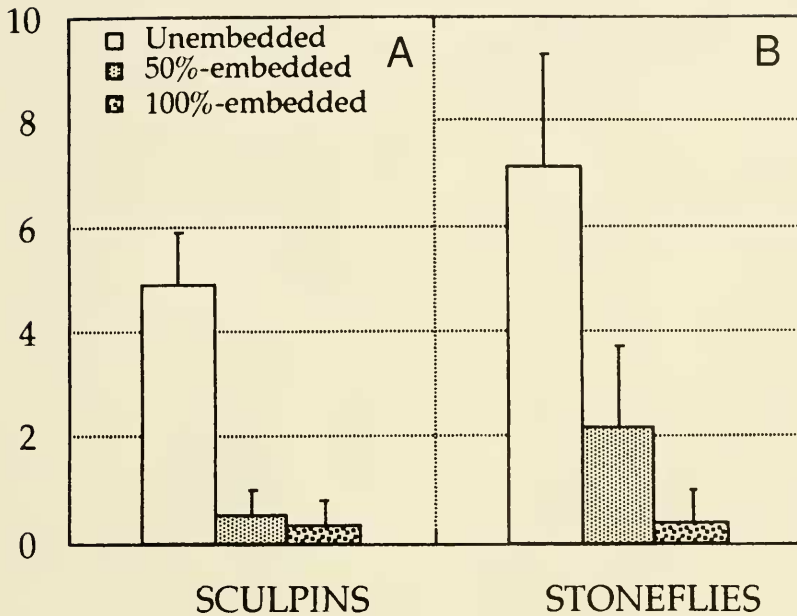


Fig. 2. Mean numbers of (A) *Cottus beldingi* and (B) *Skwala americana* recovered from three cobble-embeddedness conditions ($n = 18$) when tested noninteractively in separate stream channels. Vertical lines indicate 1 SD.

numbers in unembedded-cobble sections were significantly greater ($P < .005$) than in either the 50%- or 100%-embedded sections (Table 1, Fig. 2A); however, there was no difference in ranked sculpin numbers between the latter cobble-embedded conditions. When substrate effects were discounted, no differences were found when sculpin numbers were analyzed by stream section.

Ranked stonefly numbers were also significantly different among substrate-embeddedness conditions ($P < .001$) when tested in absence of sculpin predators (Table 1). Furthermore, all multiple comparisons between substrate conditions were significant ($P < .005$). Like sculpins, stonefly nymphs were most abundant in unembedded-cobble substrata followed by 50% and 100% cobble-embedded conditions (Fig. 2B). Nymphs were most often found on the undersides of unembedded cobbles and on the sides of 50%-embedded cobbles. As with sculpins, when substrate effects were discounted, stoneflies did not distribute themselves differentially within any particular section in the channel. At the conclusion of the experiment, nearly all (99%) stonefly nymphs introduced were recovered alive.

Predator and Prey—Interactive

When placed together, sculpins and stoneflies were distributed similarly, in proportionate numbers, among three cobble-embeddedness conditions as when tested separately (Table 1). Greatest densities of sculpins and stoneflies were in the unembedded-cobble sections (Fig. 3A, B).

Stonefly numbers were 35, 20, and 15% lower, respectively, than numbers recorded from unembedded, 50%, and 100% cobble-embedded sections without predators. Although stonefly densities were altered by predation, numbers of stoneflies occupying the unembedded-cobble substrata were more than double those found in the cobble-embedded sections during the tests conducted without predators. Furthermore, mean stonefly numbers from the 50%- and 100%-embedded substrata were nearly identical between the two experiments.

DISCUSSION

Unembedded-cobble substrata supported the highest densities of sculpins and stoneflies when tested both independently and interactively. We propose that spatial refugia afforded

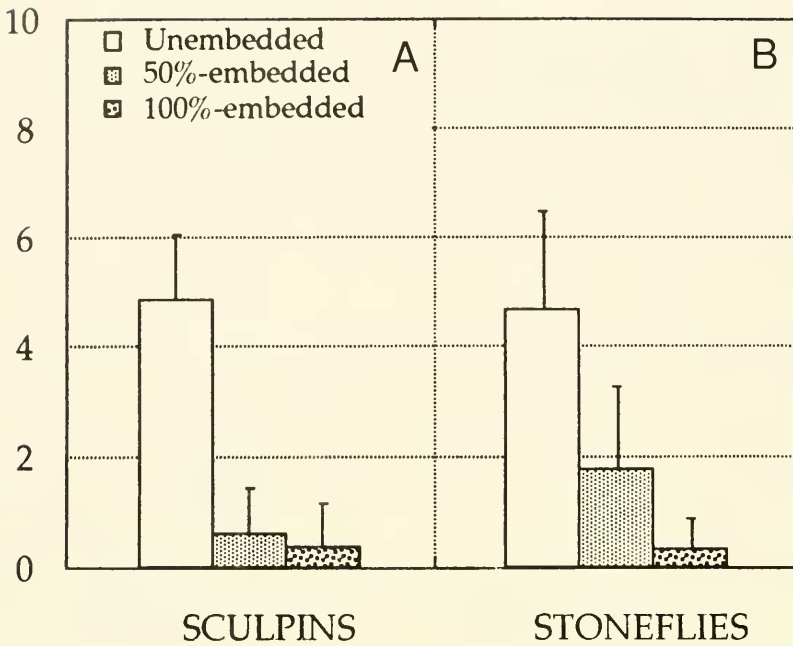


Fig. 3. Mean numbers of (A) *Cottus beldingi* and (B) *Skwala americana* recovered from three cobble-embeddedness conditions ($n = 24$) when tested interactively in streams. Vertical lines indicate 1 SD.

by the unembedded-cobble substrata influenced the distribution of *S. americana* more than the presence of vertebrate predators occupying mutually similar habitats. We submit that if the probability of prey escapement increases in unembedded cobbles because of expeditious access to refugia, then the stonefly may tolerate a greater risk of predatory attack. In theory, habitat-specific escape behavior can reinforce a prey's preference for habitats shared by coevolved predators (Lima 1992). According to Peckarsky (1982), prey that are smaller than their predators can effectively occupy interstitial spaces not habitable by predators. This hypothesis is supported by the fact that significantly more stoneflies occupied the 50%- than 100%-embedded cobble substrata, whereas sculpin densities found within these embedded substrata were nearly identical. Further, Davis and Warren (1965) found that, in a laboratory channel similar to one used in this study, prey consumption by *Cottus perplexus* significantly decreased as *Cottus* densities increased. High densities of *C. beldingi* in the unembedded-cobble substrata may have produced a similar interference response, thereby reducing the potential predation pressure on *S. americana*.

Predators have been shown to have non-lethal effects on prey by altering prey distribution (Power and Matthews 1983, Sih 1987, Kohler and McPeck 1989). However, results from our study generally do not support this type of response to predation. Our findings more closely approximate those of Sih et al. (1992), who reported that relative changes in prey density were attributed almost entirely to predation rather than predation-induced emigration.

While we did not conduct stomach analysis on the sculpin predator to confirm prey consumption in this study, earlier studies by Johnson (1985) in Lapwai Creek reported extensive predation of *S. americana* by *C. beldingi*. Accordingly, we surmised that reduced densities of prey at the conclusion of an experiment having sculpins present were due to predation alone.

In the field unembedded-cobble substrata likely offer better foraging conditions for *S. americana*, offsetting potential risks of sculpin predation. Siltation in riffle habitats reduces macroinvertebrate prey densities, especially mayflies (McClelland and Brusven 1980, Lenat et al. 1981, Peckarsky 1984), and may lower stonefly residence time within cobble-

embedded patches. Short and Ward (1980) noted that low densities of *S. americana* in a Colorado mountain stream were not the result of limited food, but of siltation from bank erosion that reduced suitable habitat.

Macroinvertebrate densities from Lapwai Creek were much lower when the cobbles were 50–75% embedded than 0–25% embedded (Haro 1988). However, differences in macroinvertebrate abundance were not so great as to suggest prey was limiting to sculpins in these cobble-embedded substrata.

In conclusion, unembedded-cobble substrata in artificial streams provided spatial refugia for macroinvertebrates from sculpin predation. Stoneflies continued to select this microhabitat even though it harbored potentially dangerous sculpin predators. Cobble substrata can be greatly altered in sediment-laden, midorder streams draining agricultural lands (Haro 1988). Cobble impaction resulting in habitat degradation may destabilize ecological relationships between organisms that have coevolved in relatively silt-free and unembedded-cobble riffles. The importance of substrate condition in mediating predator-prey interactions in streams is becoming more evident (Feltmate and Williams 1989, Gilliam et al. 1989, Fuller and Rand 1990). Thus, the mechanisms by which and the extent to which nonpoint source sediment perturbations alter lotic food-web dynamics warrant careful consideration when evaluating stream ecosystems in the future.

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